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The influence of domestication, insularity and sociality on the tempo and mode of brain size evolution in mammals

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The ability to develop complex social bonds and an increased capacity for behavioural flexibility in novel environments have both been forwarded as selective forces favouring the evolution of a large brain in mammals. However, large brains are energetically expensive, and in circumstances in which selective pressures are relaxed, e.g. on islands, smaller brains are selected for. Similar reasoning has been offered to explain the reduction of brain size in domestic species relative to their wild relatives. Herein, we assess the effect of domestication, insularity and sociality on brain size evolution at the macroevolutionary scale. Our results are based on analyses of a 426-taxon tree, including both wild species and domestic breeds. We further develop the phylogenetic ridge regression comparative method (*RRphylo*) to work with discrete variables and compare the rates (tempo) and direction (mode) of brain size evolution among categories within each of three factors (sociality, insularity and domestication). The common assertion that domestication increases the rate of brain size evolution holds true. The same does not apply to insularity. We also find support for the suggested but previously untested hypothesis that species living in medium-sized groups exhibit faster rates of brain size evolution than either solitary or herding taxa.

ADDITIONAL KEYWORDS: mammals – phenotypic evolutionary rate – *RRphylo*.

INTRODUCTION

Possessing a large, complex brain is typical of mammals (Yao *et al.*, 2012; Boddy *et al.*, 2012; Herculano-Houzel *et al.*, 2015). The evolution of such large brains is said to be promoted by a variety of factors, including high levels of sociality (Gould, 1975; Deacon, 1990; Finarelli & Flynn, 2009; Dunbar & Shultz, 2017), living in demanding or rapidly changing habitats (Mace *et al.*, 2009; Nevo *et al.*, 2009), the consumption of highly nutritious food (Aiello & Wheeler, 1995; Isler & van Schaik, 2006, 2009) and prolonged gestation length (Martin *et al.*, 2010; Barton & Capellini, 2011; Jones & MacLarnon, 2015). These factors are commonly seen as selection agents favouring large-brained individuals (Sol *et al.*, 2008; Boddy *et al.*, 2012; Benson-Amram *et al.*, 2016; Powell *et al.*, 2017). On the contrary, saving energy during growth by producing smaller brains could be adaptive where the importance of sense organs and anti-predator behaviour is de-emphasized, such as on islands (Köhler & Moyà-Solà, 2004) and in domestic species (Kruska, 2005; Zeder, 2015).

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Given that larger-bodied species have comparatively larger brains and that phylogenetically close species share similar brain sizes, analyses of brain size evolution are better conducted taking into account the effects of both phylogeny and body size. With this aim, we recently developed a new version of phylogenetic ridge regression (*RRphylo*; Castiglione *et al.*, 2018), treating body size as an additional (to phylogeny) predictor in calculating evolutionary rates of brain size (Serio *et al.*, 2019; Melchionna *et al.*, 2020).

It has been argued that the comparatively small brain of domestic mammals (Kruska, 2005; Zeder, 2015) is acquired through rapid evolution (Kruska, 1987) via artificial selection. However, this conventional view has recently been challenged by Geiger *et al.* (2018), who found no evidence of differences in the rate of evolution in comparisons of domestic pig and dog skulls with those of wild boar and wolves, respectively.

Moreover, although it is often posited that natural selection favours the evolution of smaller brains in the extinct insular goat *Myotragus* and in the fossil hippopotami of Madagascar (Köhler & Moyà-Solà, 2004; Weston & Lister, 2009), insular dwarf elephants appear to have possessed extremely large brains (Larramendi & Palombo, 2015) for their size. Likewise, the proposal that body size in insular mammals evolves quickly (Lister, 1989; Millien, 2011) has been contested on the basis of phylogenetic analyses (Raia *et al.*, 2010; Raia & Meiri, 2011), lending weight to the assertion that the rate of brain size evolution in insular species might also differ little from that of mainland populations. Consequently, the existence of a trend towards the evolution of smaller size or of faster rates of brain evolution in insular mammals is now contested.

A further factor that might influence the evolution of brain size is an increased level of sociality to facilitate the development of complex networks of relationships with conspecifics. This 'social brain hypothesis' (Dunbar, 2009) has been supported by studies of several mammalian groups (Dunbar & Shultz, 2007; Holekamp *et al.*, 2015) and birds (Lefebvre, 2013). However, there are at least some clear exceptions, e.g. solitary tigers have larger brains compared with the brains of social lions (Yamaguchi *et al.*, 2009). If the opportunity for and intensity of social learning (presumed to prompt the evolution of larger brains; Lefebvre, 2013) are correct, then we would expect that brain size would scale positively with the number of individuals within social groups (Dunbar, 2003; Dunbar & Shultz, 2007). However, the formation of particularly large and unstable herds of hundreds of individuals might provide no opportunity to learn complex behaviours and memorize past interactions with conspecifics (Shultz & Dunbar, 2005). Consequently, brain size evolution might be a non-linear function of sociality, with comparatively larger brains and faster rates of evolution accruing to species with intermediate levels of sociality.

In this study, we present and apply a further extension of multiple phylogenetic ridge regression capable of use with discrete predictors. We ask whether insularity and domestication have increased or slowed down the rate of brain size evolution in mammals, focusing on both the rate and the direction of evolution of brain size.

MATERIAL AND METHODS

Data collection

We collected data from published articles to create a dataset inclusive of brain and body mass for 426 taxa: 178 artiodactyls (six extinct, 172 extant), 26 perissodactyls (four extinct, 22 extant), ten proboscideans (eight extinct, two extant) and 212 carnivores (all extant) (Supporting Information Dataset 1). Seventy-two taxa represent domestic breeds, including pig, horse, cow, sheep, goat, cat and dog breeds. The 354 remaining taxa are wild species (Supporting Information, Dataset 2).

Where brain volume rather than mass was available, we obtained the brain weight by assuming 1036 g per 1000 cm^3 as the conversion factor (Stephan *et al.*, 1981; Rehkämper *et al.*, 1991).

We assessed the rate of change in brain size per unit body size by using phylogenetic ridge regression (see the next paragraph). To perform phylogenetic ridge regression, we modified the backbone phylogeny published by Raia & Meiri (2011; Supporting Information, File 1), adding domestic breeds to their wild relatives as polytomies. The phylogenetic tree was calibrated by using the function *scaleTree* in the R package *RRphylo*. *scaleTree* allows the tree branch lengths to be tuned by imposing specific ages at given nodes and for the terminal leaves (species). Data for tree calibration (i.e. species last appearance and internal node ages) are available as Supporting Information, Dataset 3.

We assessed the effects of three factors proposed to affect brain size variation between species: domestication, insularity and sociality. We considered as insular species those occurring exclusively on islands, provided the island was smaller than Australia, i.e. up to the size of New Guinea (785 753 km^2). The insularity category includes 19 species, both extinct (i.e. *Elephas falconeri*) and extant, and 407 mainland species. Data for insularity status were taken from the studies by Raia *et al.* (2010) and Raia & Meiri (2011).

Species in the tree were classified further according to four categories, representing increasing levels of sociality according to *Walker's Mammals of the World* (Nowak & Walker 1999). supplemented with additional sources as specified in the Supporting Information (Dataset 2). Species whose individuals spend most of their lifetime as solitary (or as solitary mothers and their offspring) were classified as 'solitary'. Species living in groups of up to ten individuals for most of their lives were placed in the 'family' category. Species whose individuals live in groups of 11–30 individuals were categorized as members of a 'group'. Finally, species whose individuals live in groups of > 30 individuals were considered as members of a 'herd'. The criteria we used for categorizing social groups are somewhat arbitrary, given that group size is not fixed and can vary depending on the breeding season and changes in the availability of resources. Thus, although we felt that our categorization captured the essential information that levels of social interactions increase with group size, we produced a second categorization, whereby species living in pairs (of a breeding male and a female) staying together outside the breeding season are tallied as 'pair'. One further potential problem with the sociality classification is that domestic animals live in unnatural groups confined to closed areas for husbandry. Therefore, we repeated the sociality analyses excluding domestic breeds.

Phylogenetic multiple regression with

To study the evolution of brain size while accounting for the effect of phylogeny, body size and the three factors being tested (i.e. domestication, insularity and sociality), we used the *RRphylo* R package toolkit. The package main function, *RRphylo*, is a phylogenetic comparative method for performing phylogenetic ridge regression on a phylogenetic tree and phenotypic data to return branch-wise rates of phenotypic evolution and ancestral estimates at internal nodes (Castiglione *et al.*, 2018). The multiple regression version of *RRphylo* allows incorporation of the effect of an additional predictor (e.g. phenotypic variable or ecological factor) on the calculation of the evolutionary rates, which are thus estimated as:

$$(\boldsymbol{L}'^T\boldsymbol{L}' + \lambda\boldsymbol{I})^{-1}\boldsymbol{L}'^T Y$$

where L' is the matrix of branch lengths intervening between each tip and the nodes along its path, supplemented with the predictors as columns (i.e. as many columns as the number of predictors); the superscript T indicates the transpose of the matrix; y is the vector of the phenotypic variable under test; λ is the normalization factor optimized to avoid abnormal rate values; and $\boldsymbol{I}$ is the identity matrix. Thus, as with a single predictor, the last elements (as many as the number of predictors) of the $\hat{\beta}$ vector of phenotypic rates represent the partial ridge regression coefficients of the predictors.

One crucial advantage of using *RRphylo* is that it allows us to test whether the phenotype under scrutiny evolves at different rates in different parts of the phylogeny, or for species evolving under different regimens, which is most likely to be the case with the factors we tested here.

Herein, we implemented this method further to include additional predictor variables at the same time and to deal with categorical predictors. To test the accuracy of *RRphylo* at deriving sensible estimates of ancestral states for categorical variables, we compared the outcomes of *RRphylo* with existing methods to estimate ancestral categorical states. Both *ace* and *make.simmap* functions, available in the R packages ape (Paradis & Schliep 2018) and phytools (Revell, 2012), respectively, provide the maximum likelihood probabilities of each node being in each state according to stochastic character mapping. *RRphylo* predictions were compared with the other two methods by applying a Random Forest algorithm (Breiman, 2001; for details, see Supporting Information, File 2, Table S1; to replicate the testing, see Supporting Information, Code 1).

Multiple regression *RRphylo* computes the rates of brain size evolution accounting for body size. Although this is sound to study rates (i.e. the evolutionary tempo), the method does not account for the effect of the predictor on brain size (i.e. the evolutionary mode). With this aim, for each factor, we assessed differences in brain size among categories while accounting for phylogenetic effects by means of the function *phylANOVA* in phytools (Revell, 2012). *phylANOVA* assumes the Brownian motion model of evolution, i.e. a single evolutionary rate persisting throughout the tree, which is most probably violated by the effects of domestication, sociality and, possibly, insularity. To verify the assumption that the evolution of brain size occurred in accordance with the predictions of the Brownian motion model, we computed the phylogenetic signal, calculating Blomberg's K statistic (at $K = 0$ there is no phylogenetic signal in the data; at $K = 1$ the phenotypic distribution coincides with the Brownian motion predictions), using the function *physignal* within the package geomorph (Adams & Otárola Castillo, 2013). Given that we found that the Brownian motion assumption was violated, we modified the input data in *phylANOVA* to account for rate variation. We initially resolved polytomous clades, adding zero-length branch nodes with the function *multi2di* in the package ape. Next, we ran *RRphylo* by using the natural logarithm (ln) of brain size and the natural logarithm of body size as response and predictor variables, respectively. Then, we rescaled the original phylogeny by multiplying each branch by its own absolute rate value. The rescaled phylogeny was used in *phylANOVA* to account for phylogenetic effects.

Differences in evolutionary rates of brain size among categories within individual factors were assessed by means of the function *search.shift* from the RRphylo package (Castiglione *et al.*, 2018). When contrasting evolutionary rates among different states dispersed across different clades in the tree (i.e. the 'sparse' condition), *search.shift* compares the average absolute rate computed for the species in a given state with the average rate of the rest of the tree and assesses significance by means of randomization. For each factor, we computed rates of evolution of brain size by performing the multiple regression version of *RRphylo* using the natural logarithm of brain size as the response and the natural logarithm of body size along with the factor as the predictors. The result of each *RRphylo* was fed to *search.shift* to look for differences in rate among different categories for each factor (i.e. domestication, insularity and sociality). In the case of sociality, the analyses were repeated on the tree deprived of domestic species.

The addition of domestic species (in the form of distinct breeds of dogs, pigs, horses, cattle and sheep) introduces phylogenetic uncertainty, because their phylogenetic history is poorly defined and further complicated by secondary contacts and gene flow between different breeds and specific breeds and wild individuals. With so much phylogenetic uncertainty, domestic species must be placed on the tree as soft polytomies (i.e. a comb-like tree) along with their wild relatives. Although reasonable, this implies unrealistically long branch lengths for the domestics, because it effectively assumes that all breeds appeared together at the time of the first domestication event. This assumption would bias the calculation of evolutionary rates, because these represent phenotypic change per unit time. To correct for this, we implemented a new function, *fix.poly*, which resolves polytomies randomly, adding nodes within the polytomous clade while keeping fixed the time distance from the root for individual tips and their common ancestor. To account for the effect of the random dichotomization within *fix.poly*, we replicated the whole set of analyses 100 times on as many different dichotomic phylogenies.

RESULTS

EVOLUTIONARY TEMPO OF BRAIN SIZE EVOLUTION

The absolute rates of evolution of brain size computed by accounting for the effect of body size and domestication were significantly different between wild and domestic species, with the latter evolving more quickly towards smaller brain size (i.e. negative rate difference; Table 1; Fig. 1). This outcome was supported by the analysis replicated on the resolved trees (100% significant and negative differences between wild and domestic species).

The comparison of rates of evolution of brain size between insularity categories (computed in a multiple regression framework, with body size and insularity as predictors) returned no significant difference for the original tree and for the resolved trees (Table 1; Fig. 2).

Regarding the rates of evolution of brain size computed by accounting for the effect of body size and sociality, the rate of 'solitary' species was significantly lower than the rate obtained for the rest of the tree, by using either the original tree or the resolved phylogenies (Table 2; Fig. 3). The reverse characterized species living in family groups ('family'). These showed the highest absolute rate of evolution of brain size, irrespective of the phylogeny used (Table 2). Species belonging to the 'group' category showed no significant absolute difference in rate from the rest of the original tree, and resolved phylogenies provided 15% significant and positive results (Table 2). The absolute brain size evolutionary rates for 'herd' species were significantly lower than the rates of the rest of the original tree (Table 2). This was also true for 65% resolved phylogenies.

Comparisons of absolute rates between social categories revealed that 'solitary' species evolve more slowly and 'family' species faster, in terms of brain size, compared with the rest of the tree. The difference between these categories was always significant, irrespective of the tree used (Table 2). Brains for the species in the 'family' category also evolved faster than those of the 'group' and 'herd' species. This held true when accounting for phylogenetic uncertainty in 73 and 99% of the cases (Table 2). The addition of the 'pairs' level in social category 2 did not change these results. Brains of the species in the 'family' category, however, evolved faster than in 'pairs' species (Table 2).

Table 1. Brain size evolutionary rate comparison for species classified according to domestication and insularity status

Status	Rate difference	*P*-value	% resolved trees
Wild–domestic	–0.427	**0.001**	100
Mainland–insular	0.130	0.927	0

Rate difference is the average absolute rate difference computed by using the original tree; *P*-value is the significance level for the rate difference; % resolved trees is the the percentage of *search.shift* as performed on the phylogenies resolved by *fix.poly* that produce significant results. The 5% significance level is represented by *P*-value < 0.025 and *P*-value > 0.975. Significant result is in bold type.

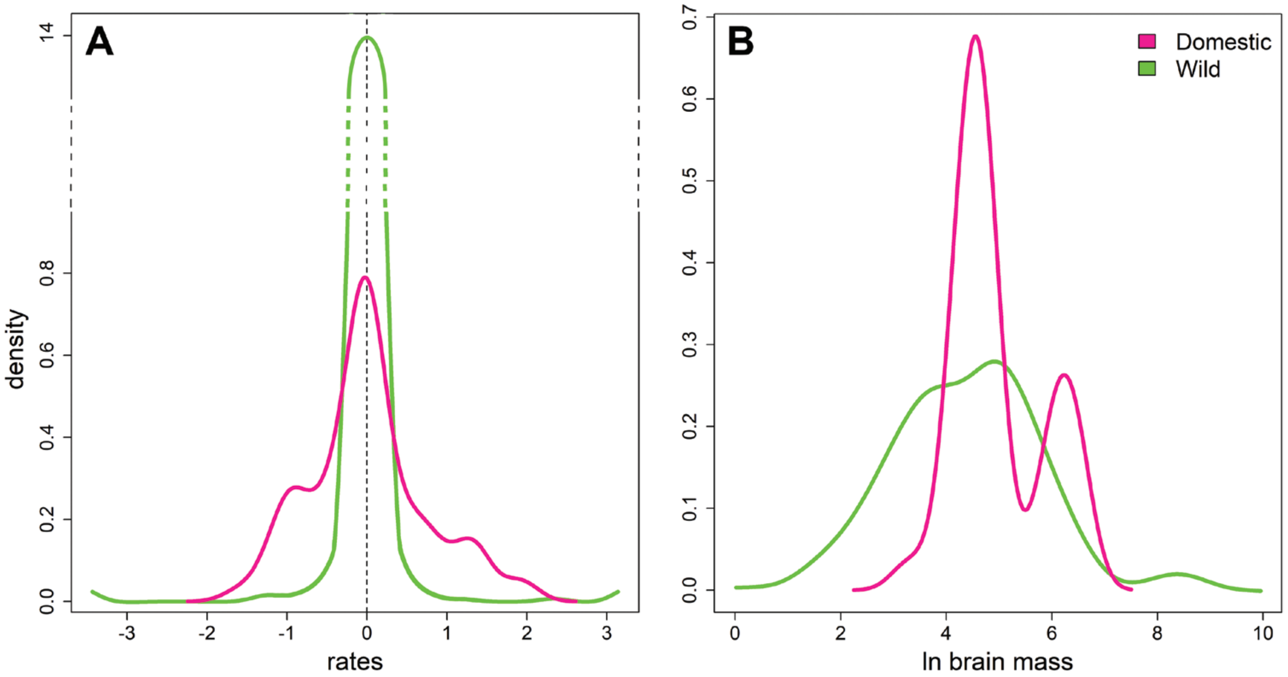

Figure 1. Density plot of brain size evolutionary rates (A) and weight (B; in ln grams) computed by accounting for the effect of body size and domestication. The vertical dashed line in A indicates the zero-rate line.

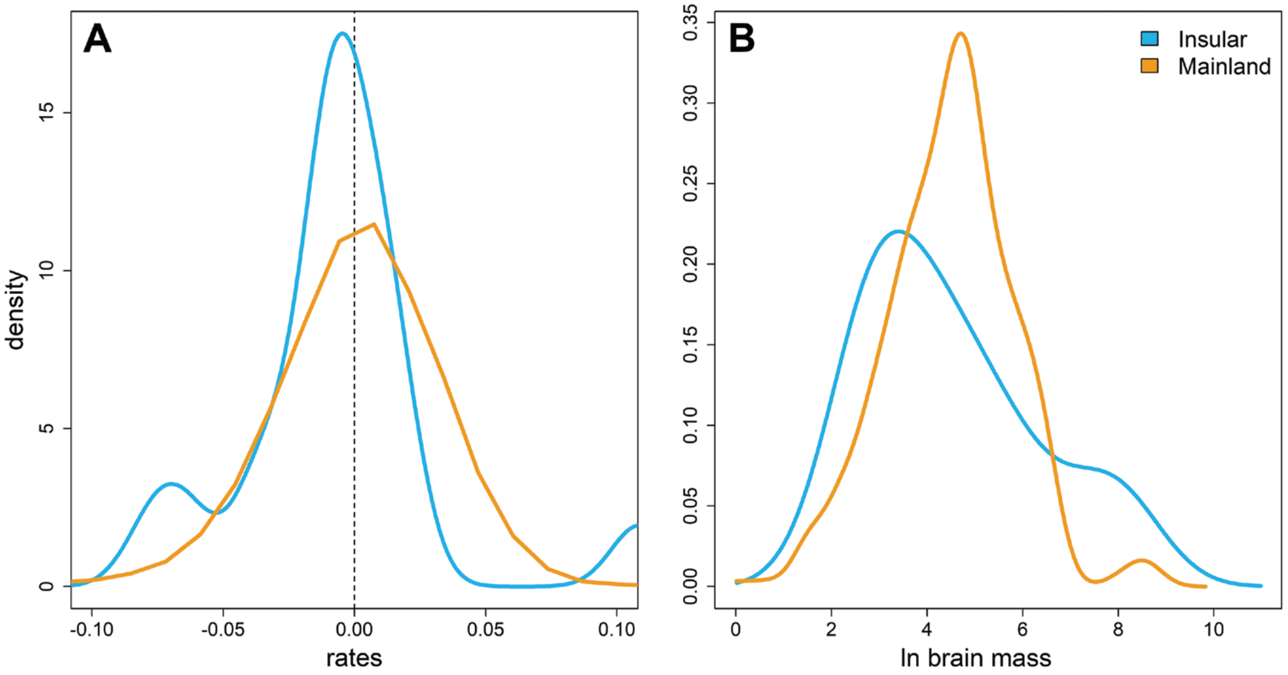

Figure 2. Density plot of brain size evolutionary rates (A) and weight (B; in ln grams) computed by accounting for the effect of body size and insularity. The vertical dashed line in A indicates the zero-rate line.

Table 2. Brain size evolutionary rate comparison for species classified according to four (social category 1) or five (social category 2) categories of increasing sociality levels

	Social category 1			Social category 2		
Status	Rate difference	*P*-value	% resolved trees	Rate difference	*P*-value	% resolved trees
Solitary	−0.229	**0.001**	100	−0.213	**0.001**	100
Pairs	–	–	–	−0.078	0.123	14
Family	0.299	**1.000**	100	0.358	**1.000**	100
Group	−0.006	0.502	0	−0.013	0.474	0
Herd	−0.022	0.427	0	−0.025	0.385	0
Pairs–solitary	–	–	–	0.071	0.813	0
Family–solitary	0.348	**1.000**	100	0.417	**1.000**	100
Group–solitary	0.127	0.962	71	0.127	0.956	60
Herd–solitary	0.113	0.941	16	0.117	0.930	6
Family–pairs	–	–	–	0.346	**1.000**	100
Group–pairs	–	–	–	0.056	0.754	1
Herd–pairs	–	–	–	0.046	0.675	0
Group–family	−0.222	**0.001**	73	−0.290	**0.001**	95
Herd–family	−0.235	**0.001**	99	−0.300	**0.001**	100
Herd–group	−0.014	0.450	0	−0.010	0.441	0

Each category is contrasted with the rest of the tree and with the other categories. Rate difference is the average absolute rate difference computed by using the original tree; *P*-value is the significance level for the rate difference; % resolved trees is the the percentage of *search.shift* as performed on the phylogenies resolved by *fix.poly* that produce significant results. The 5% significance level is represented by *P*-values < 0.025 and > 0.975. Significant results are in bold type.

When domestic species were excluded, 'family' species remained the fastest (and 'solitary' the slowest) in terms of the rate of evolution of brain size, irrespective of the phylogenetic topology and branch lengths used (Supporting Information, Table S2).

EVOLUTIONARY MODE OF BRAIN SIZE EVOLUTION

The phylogenetic signal for the natural logarithm of brain size was low and significantly different from one ($K = 0.088$, $P = 0.001$). The average phylogenetic signal retrieved by using resolved trees was 0.039 (95% confidence interval: 0.029–0.049) and was always significantly different from one. These results indicate that brain size evolution was inconsistent with the Brownian motion model of evolution.

The phylogenetic ANOVA performed on the natural logarithm of brain size and the original tree comparing domestic vs. wild species produced no significant difference (Table 3). The replications performed on the resolved phylogenies provided the same results in 100% of cases (i.e. 0% of significant differences; Table 3). The comparison of the natural logarithm of brain size between insular and mainland species was not significant by using the original trees or any of the resolved trees (Table 3).

Brain size was smaller, on average, for solitary than for social species (Table 4). Results of *phylANOVA* indicated that there was a significant difference in brain size among social categories, irrespective of whether the original or the resolved trees were used (Table 5). For the original tree, the pairwise comparison between social groups produced significant differences between 'group' and 'herd' species compared with 'solitary' taxa. By using social category 2, this also applied when comparing 'group' and 'herd' species with 'pairs' taxa (Table 5).

When domestic species were excluded, global differences in brain size among social categories were still apparent, meaning that there was an increase in brain size with increasing levels of sociality (Supporting Information, Table S3).

DISCUSSION

Our findings show that domestication and sociality have profound and significant effects on rates of evolution of brain size, whereas insularity does not. To our knowledge, this is the first study to demonstrate quantitatively that artificial selection (domestication) drives faster rates of brain evolution than does natural selection at the macroevolutionary level, after controlling simultaneously for body size and phylogeny. This contrasts with the recent study which found that evolutionary rates did not differ significantly between domestic and wild animals (wild boar/pig and wolf/dog; Geiger *et al.*, 2018).

On the basis of brain size, the median *RRphylo* rate in domestic species is negative (−0.0012; Fig. 1). Given

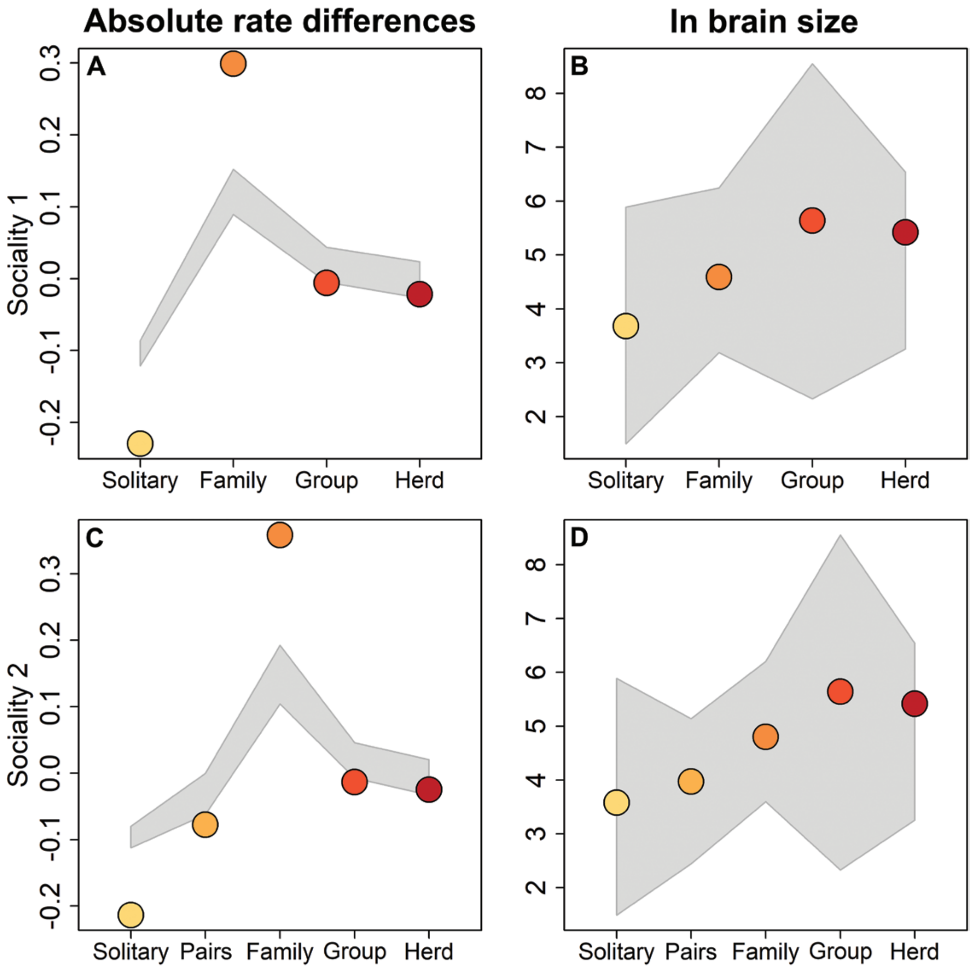

Figure 3. Difference between the average brain size absolute rate (A, C) and weight (B, D; in ln grams) computed for each social factor and the average rate for the rest of the tree. Coloured circles represent absolute rate differences retrieved by using the original tree. The shaded grey area depicts the range of absolute rate differences as derived by replicating the analyses on 100 resolved phylogenies (A, C) and confidence intervals around average brain size per category (B, D).

that *RRphylo* rates are regression slopes between consecutive nodes in the phylogeny, this indicates that there is an average tendency for brain size to decrease in domesticated mammals, whereas in wild species the median rate is positive (0.0024; Fig. 1). Although domestic breeds tend to have smaller brains than their wild relatives, this is not equally evident across all domesticated species, and the reduction is much more apparent in artiodactyls (i.e. livestock; Heck *et al.*, 2018). This inconsistency explains why brain size does differ not significantly between domestic and wild forms, according to phylogenetic ANOVA. One potential factor confounding the difference between wild and domestic species in terms of brain size is sociality and the type of interaction that domestic breeds have with humans. Most livestock gather in herds, exposed to reduced social stimuli, and are sometimes even killed for commercial purposes before maturity, whereas

Table 3. Average natural logarithm of brain mass and results of phylogenetic ANOVA: average natural logarithm of brain mass, 95% confidence intervals and significance level of phylogenetic ANOVA performed by using domestication or insularity as predictors

Status	Mean brain mass	95% Confidence interval	Phylogenetic ANOVA	
			Original tree	% resolved trees
Wild	4.388	1.573–7.426	0.373	0
Domestic	4.959	3.856–6.532		
Mainland	4.483	1.656–6.610	0.946	0
Insular	4.516	2.390–8.082		

Original tree is the *P*-value computed by performing the phylogenetic ANOVA on the original tree; % resolved trees is the the percentage of phylogenetic ANOVAs as performed on the resolved phylogenies that produce significant results.

pet animals (i.e. dogs and cats in our dataset) are commonly raised in continuous interaction with their owners, implying richer psychological experiences during growth for these carnivores, in comparison to the herbivorous species (Heck *et al.*, 2018). However, other studies have found that, with the exception of pigs, the reduction in brain size in domestic animals does not differ between carnivores and herbivores (Driscoll *et al.*, 2009; Zeder, 2015). Furthermore, the extent of reduction of brain size in domestic sheep, goats and horses is difficult to determine with our data. This is because, for these clades, it is difficult to identify 'wild' representatives for which gene flow with domestic individuals was limited. Consequently, although our results are consistent with the traditional view that the rate of evolution of brain size is faster in domestic species (Kruska, 1987), the lack of significant phenotypic difference might be influenced by limitations in the dataset.

Mammalian species confined on islands often live in species-poor ecosystems and tend to be herbivores. An apparently frequent set of phenotypic transformations shared by these insular 'ungulates' is the loss of antipredator behaviours and reductions in body and brain size (Köhler & Moyà-Solà, 2004; Weston & Lister, 2009). Although clearly common, the tendency toward brain size reduction is reversed in insular dwarf elephants (Larramendi & Palombo, 2015) and, most notably, does not apply to *Homo floresiensis*, the smallest-brained hominid ever described (Diniz-Filho & Raia, 2017; Diniz-Filho *et al.*, 2019). These results are consistent with recent evidence that insular vertebrates do not evolve to either extreme of body size compared with their mainland relatives (Meiri *et al.*, 2010), nor do they achieve comparable evolutionary rates (Raia & Meiri, 2011).

We found that sociality exerts a strong influence on the trajectories and rates of brain size evolution. 'Family' species consistently present the highest rates of evolution of brain size. Shultz & Dunbar (2005) observed that although variation in brain size in 'ungulates' conforms with the social brain hypothesis,

Table 4. Average natural logarithm of brain mass and results of phylogenetic ANOVA: mean natural logarithm of brain mass and 95% confidence interval per social category by using either four or five different levels of sociality

Status	Social category 1		Social category 2	
	Mean brain mass	95% Confidence interval	Mean brain mass	95% Confidence interval
Solitary	3.681	1.500–5.892	3.578	1.492–5.890
Pairs	–	–	3.971	2.442–5.140
Family	4.594	3.189–6.244	4.803	3.596–6.202
Group	5.639	2.331–8.551	5.639	2.331–8.551
Herd	5.419	3.256–6.538	5.419	3.256–6.538

Table 5. Average natural logarithm of brain mass and results of phylogenetic ANOVA: *P*-values for the global phylogenetic ANOVA model and for the pairwise comparison between social categories (either four or five levels)

Status	Social category 1		Social category 2	
	Original tree	% resolved trees	Original tree	% resolved trees
Global	**0.002**	100	**0.001**	100
Pairs–solitary	–	–	0.972	0
Family–solitary	0.224	0	0.135	0
Group–solitary	**0.006**	100	**0.010**	100
Herd–solitary	**0.020**	100	**0.028**	34
Family–pairs	–	–	0.054	16
Group–pairs	–	–	**0.010**	100
Herd–pairs	–	–	**0.010**	100
Group–family	0.224	0	0.444	0
Herd–family	0.384	0	0.972	0
Herd–group	0.674	0	0.972	0

Original tree is the *P*-value computed by performing the phylogenetic ANOVA on the original tree; % resolved trees is the the percentage of phylogenetic ANOVAs as performed on the resolved phylogenies that produce significant results. Significant results are in bold type.

large, commonly ephemeral ungulate herds leave little room for the formation of long-lasting social bonds, perhaps explaining why herd species are the least influenced (together with solitary species) by the 'social brain effect'. Our results are entirely consistent with this proposition and are supportive of the positive link between complexity of social interactions and brain evolution that is at the core of the social brain hypothesis.

In conclusion, the results of our analyses conducted at macroevolutionary scales are consistent with the longstanding hypothesis, previously tested only at limited levels, that domestication elevates evolutionary rates (toward a reduction in brain size). We find that insularity has no effect on the evolution of brain size at macroevolutionary levels but find support for the hypothesis that species living in medium-sized groups are characterized by faster evolution in brain size than either solitary or herding taxa.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Percentage error rates as retrieved by using Random forest algorithm for simulations with two-, three-, and four-states categories. B) mean and 95% confidence intervals for regression intercepts and slopes of simulated versus estimated (by *RRphylo*) ancestral categorical characters for two-, three-, and four-states categories.

Table S2. Results of brain size evolutionary rates comparison between social categories for species classified in four or five different levels after excluding domestic species from the data. Each category is contrasted to the rest of the tree and to the other categories. rate difference = average absolute rate difference computed by using the original tree; *P*-value = significance level for the rate difference; % resolved trees = the percentage of *search.shift* as performed on the phylogenies resolved by *fix.poly* which produce significant results. 5% significance level is represented by P-value < 0.025 and P-value > 0.975.

Table S3. Average ln brain mass, 95% confidence interval, and results of phylogenetic ANOVA by using sociality as predictor after excluding domestic species from the data. A. Mean ln brain mass and 95% confidence interval per social category by using either four or five different levels. B. P-values for the global phylogenetic ANOVA model and for the pairwise comparison between social categories (either four or five levels). original tree = P-value computed by performing the phylogenetic ANOVA on the original tree dichotomized by adding zero-length branch nodes; % resolved trees = the percentage of phylogenetic ANOVAs as performed on the phylogenies resolved by *fix.poly* which produce significant results.

File 1. Phylogenetic tree in Newick format.

File 2. Supplementary Methods and Results Tables S1, S2, and S3 are embedded in File 2.

Dataset 1. Brain mass and body mass for each species, with references for source data.

Dataset 2. Domestication, Insularity and Sociality categories for each species, with references for source data.

Dataset 3. The phylogenetic tree calibration dates, with references for source data.

Code 1. R code for testing the performance of *RRphylo* with categorical predictors.